TRANSACTIONS OF

THE ROYAL SOCIETY OF CANADA

SECTION V
BIOLOGICAL SCIENCES

THIRD SERIES—VOLUME L—SECTION V

JUNE, 1956

OTTAWA
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VOLUME L : SERIES III : JUNE, 1956

SECTION FIVE

PRESIDENTIAL ADDRESS

Conservation and Survival

GEORGES MAHEUX, F.R.S.C.

LES règlements imposent au président de cette section une sorte de devoir de dernière heure, celui de prononcer un discours avant la fin de son terme d'office. Il est, par ailleurs, de tradition que ce discours ait pour objet certaines recherches poursuivies par l'auteur au cours de sa carrière, ou une synthèse de ses travaux. Mon intention première a été de respecter la tradition. Certes, il m'eut été facile de remonter à quinze ou trente ans en arrière et de choisir comme thème de ce discours certaines recherches, que mes collaborateurs et moi-même avons menées à bien dans le champ de l'entomologie agricole.

But, in so doing I had the impression that, playing for once the rôle of an archaeologist, I would be exhuming from cold ashes some kind of relic. Moreover, entomologists of a more recent era have gone so far in the pursuit of knowledge that the adventures of an old-fashioned naturalist might appear to them as elementary endeavours.

Eloigné des recherches actives depuis plusieurs années déjà, absorbé plutôt par des tâches qui me permettent surtout de faciliter aux jeunes l'accès aux études supérieures et de leur assurer des instruments de travail dans le champ de la recherche scientifique, je crois plus sage de me tourner vers l'avenir et d'examiner quelques aspects de cette forme moderne de biologie appliquée connue aujourd'hui sous le nom de Conservation. Ce discours pourrait être intitulé: "Les ressources naturelles et la survivance de l'Humanité."

Before attacking this subject, allow me to recall the names of those entomologists who have formerly occupied the presidency of this section: James Fletcher, the genial and dynamic pioneer of applied entomology in Canada; Gordon Hewitt, who introduced here the biological control of injurious insects; James Malcolm Swaine, the founder of forest entomology in this country, to me a great master and a dear friend, who died recently; Dr. Edmund Walker, the dean of this section, a taxonomist of wide reputation, who is still very active in his laboratory at the University of Toronto.

One hundred and fifty years ago, a political economist by the name of Rev. T. R. Malthus wrote something of utmost significance to mankind in a well-known book—*Essay on the Principle of Population*—which appeared

in its definitive form in 1803. Essentially, Malthus held that "population tends to multiply faster than its means of subsistence can be made to do, and that when this occurs the lower or weaker classes must suffer from lack of food." Developing this statement he made it clear that the world population would double within a century and from then on poverty would become more and more widespread throughout the world.

The *Essay* described conditions that have consistently grown worse since it was published. For the first time, I believe, a scholar was worried about the future of humanity, and he scrutinized it with such acuity that what he foresaw happened exactly as he predicted. We have not been accustomed to hear economists expressing themselves with that precision or forecasting a century ahead. Obviously Malthus is an outstanding exception; in fact, the situation he perceived on the far distant horizon now prevails over more than half the surface of the earth.

The race of prophets and seers is rather depleted nowadays. Malthus is probably the only one in recent times, perhaps the last of the species. His long-term prediction is nothing short of a prophecy, a prophecy which is of tremendous concern to man. It measures in terms of years the precarious state of nations in times to come; it constitutes an evident presage of the decline of humanity. Finally, Malthus points out the basic factors that will gradually bring about a crucial era for mankind. Only a genuine prophet could interpret so precisely the obscure signs in the sky. Envisaged in this light, Malthus' theory forms the very basis of conservation. Therefore, the clairvoyant writer might justly be named the father of conservation, even if the word conservation, in its actual acceptation, was unknown in his days.

Recently, his prediction, after a long period of slumber in the silence of his book, has suddenly exploded with thundering effect. Anxiety over the future of humanity is spreading far and wide, as shown by the works written in recent years on that alarming subject by scores of brilliant biologists and naturalists. In each one the reader finds ample proof of the wisdom of the British economist. As a perfectly planned drama, the prophecy is fully realized under our own eyes. World population has doubled within a century since Malthus' *Essay*. Moreover, students of demography figure out that the multitude of human beings will double again in less than one hundred years, reaching four billions soon after the beginning of the twenty-first century. Thus, what we may term the "future" of humanity is no longer a remote issue; it is taking shape right now; it is rising into view.

The symptoms of the dark days to come are many and obvious. Food production on the surface of the depleted planet—despite scientific discoveries and their application to agriculture—is dangerously lagging. "It follows an arithmetic progression," wrote Malthus, "while population increases at a geometrical progression." And we might repeat here the warning voiced by Roger Heim, director of the Paris National Museum:

"Les peuples sous-alimentés ne seront pas nourris par un miracle de la science."

How many nations are today overcrowded, poorer, suffering from malnutrition, living in a far more miserable condition than a century ago! The problem is one of great concern; yet the world is just beginning to comprehend the potential and already disastrous effects it implies. No less than the gigantic clash of World War II was necessary to shake up human indifference and open the eyes of some national leaders. Realizing the tremendous importance of the problem, these clear-sighted men sensed the oncoming tragedy and strove to set up an international organization to the measure of human brotherhood, the Food and Agriculture Organization, for the specific purpose of finding and disseminating remedies to combat want and hunger all over the world. The F.A.O. is fortunately not a political undertaking, but a crusade of vital consequence to the whole world population.

With the advent of the F.A.O., the world has entered a new age, the *age of conservation*; in other words, the age of wise use or even restoration of resources provided by nature to maintain life on the surface of the earth. It would be out of place to discourse here on the aims and methods of conservation. To us, biologists, conservation is a *carrefour* where all scientific disciplines having to do with living organisms congregate to devise means to fight hunger, defend or restore health, and check everywhere the physical and social decadence of individuals, societies, and nations. To that end, we must revert to nature to learn the lessons of everlasting wisdom she teaches us. Conservation of soil, forests, and water forms in this undertaking an indivisible trinity. The study of the complex interrelations of these three, of the environmental factors, has given birth to a new science, that of ecology. No worthwhile and lasting solution can be found unless each problem of conservation is scrutinized in the light of ecological findings.

Professor Roger Heim has clearly outlined the rôle of ecology when he said: "L'Ecologie reste à la base des problèmes posés par la protection du manteau végétal, du sol qui le supporte, de la faune qui l'utilise. Elle est indispensable à la mise au point des solutions qui ne sauraient ignorer aucun des facteurs dont le jeu règle les équilibres et les déséquilibres de la Nature, à commencer par le facteur humain." Conservation must carefully study and appraise, according to Jean-Paul Harroy (former Secretary of the International Union for the Protection of Nature), "les nombreux phénomènes d'appauvrissement et d'altérations que les associations ou groupements naturels de la Planète subissent à un rythme dangereusement croissant, du fait de l'augmentation de la population humaine, sur tous les continents, et de l'intensification des prélèvements, éliminations et perturbations de toutes sortes imposées à ces associations par l'économie contemporaine."

Now, we might wonder why humanity has taken such a long time to

perceive a reality that meant its own survival or its doom. Contrary to what happens in animal populations, humanity suffers from acute short-sightedness; truly it seems a disease peculiar to man. Ruins of empires, the passing away of prosperous nations, have not impressed the successive generations, very likely because these strange events are generally considered by historians as the ultimate result of armed conflicts between nations, when in reality war has been up to now a sporadic plague inflicting cruel yet rapidly healed wounds. Thus centuries have passed before such tragedies were linked to their real cause: the depletion, abuse, and destruction of natural resources.

People living in new countries, such as ours, where the myth of inexhaustible resources is difficult to eradicate, are to a certain degree excusable if they do not see, and do not care to see, the end of their happy days. The next generations are naïvely supposed to enjoy the same happiness. It is then the privilege and the duty of a better-informed minority to enlighten the people and awaken their conscience.

It may seem a trifle odd to insist on conservation in a country where surpluses of food—at least certain foods—take the form of a chronic disease. This situation should not worry anyone who is more concerned with the future than with the present. Conservationists and biologists are aware that situations of that sort are essentially transitory. Even the mountains of wheat in the Prairies will soon be wiped out merely as a result of the population increase in Canada, a population very likely to double before the dawn of the twenty-first century.

We may learn from history how fast ill-managed, abusively used living resources can be ruined. What has become of the smiling face of Ancient Greece, described by poets as a land of plenty "where honey was flowing down the slopes of Mount Hymettus"? After thirty centuries it is a pale face, with tortured features, bearing the ugly gashes left by deforestation and erosion. Are men of today wiser than their predecessors? Must we recall that even in our days eager men are exhausting the land, plundering the forest, and leaving behind nothing but deserts? Man-made deserts have been created in Iran by greedy landlords not later than the beginning of the present century. A well-known authority on conservation, Dr. H. H. Bennett, proves what a fragile treasure is the soil that nourishes humanity when he states that in the United States, within a few years after World War I, extensive areas of fertile soil were completely exhausted to the point where they can hardly grow scattered weeds.

But instead of insisting on what you all know, let us rather consider for a few moments some of the obstacles which must be suppressed before conservation is understood, accepted as an urgent necessity, made a fundamental policy, and then strictly enforced.

In this period of transition between abundance and scarcity, many concepts must be revised and adjusted to present and future conditions; for nstance, what place biology really occupies. Though we live in times when

the fate of humanity is being decided, biology, a first requirement for future human survival and welfare, is still considered by a huge majority of people from all ranks as a mere accessory in matters of national economy, public administration, legislation, and so on. It appears that we live in a period of contradictions because our society is erected on an obsolete substructure. Biology, science of life, unique instrument for the survival of man, should logically be the underlying principle of any legislation pertaining to natural or material matters. A revision of the legislation, as its very basis, is therefore imperative. A revision of economic concepts is also in order. They should be revised but not, as usual, in view of short-term effects upon the population, not with the strong accent on accessory matters. They should be revised on terms of human survival, in terms of natural values which alone can make possible this survival.

The first concern of any government, in its policy and economy, is to base its calculations on the welfare of future generations in the projection of time. For once, a royal commission is presently at work striving to foresee or shape the economic pattern of Canada twenty-five years from now. This is good news; it shows a worthwhile improvement over what usually took place in the past. Some governments have tackled the problem, as should be done. They have devised the necessary machinery to restore the biological balance in their territories; they are even rebuilding what was partially destroyed by past generations. These real statesmen are deserving of full appreciation from biologists. Yet Canada is still lacking a national conservation policy, a plan that would embrace the whole country with a view to checking any further depletion and taking means to increase, with the help of biological research, the yield of our soil, forests, water, fish, and game resources. The treasure of the nation must be preserved at any cost and made permanent.

The methods of using natural resources on this new continent must also be revised. A century of intensive development has shown us in too many instances that the blindness of capital and the eagerness of some industries have dangerously shaken the security of nations and endangered their future. The disappearance already of many industries directly connected with natural resources is ample proof of a lamentable squandering.

A revision of the right of property, that is, the exercise of this right, is also required. As defined and protected by actual laws, it is certainly out of date. It originated with the Greek and Roman civilizations when resources of all sorts were plentiful and the population of the world exceedingly restricted compared with that of today. The exercise of the right of property should, of necessity, be first of all subordinated to the interests of the nation, which must supersede any particular interest. Of course, there are now some legal limitations, but they are one-sided and ignore other essential matters. For instance, you cannot operate a still on your farm; but the law will not interfere if you ruin the land, deforest steep slopes, provoke erosion from which acres of farmlands may be seriously damaged. This conflict

between personal and national interests has been clearly exposed by a well-known advocate of conservation, Dr. D. B. Turner, in "Selling Conservation by Conference." "Conflicts of interests," writes Dr. Turner, "may arise between the philosophy of personal welfare, which characterizes the individual, and the collective advantages which inspire society. What is at stake in such conflicts is nothing else than the richness of our soils, our forests, our water, our other natural resources." (Translated from a French quotation.)

An unwritten rule, though a prevailing one, seems to urge individuals and communities to carry out anti-natural or anti-national practices with the unanimous consent of everyone concerned. Examples of such widespread folly may be witnessed everywhere. The good soil, the most precious treasure of humanity, is treated as a negligible thing, in times of superabundance; you see it disappearing at the rate of many thousands of acres each year to make room for industrial or housing developments in suburban areas, while poor soils nearby are left undisturbed. The net result is that the nation is gradually deprived of an important source of food production.

How often public works, achieved under the sign of improvement of human conditions, bring about exactly opposite results. For instance, man dangerously plays with water resources when he drains certain lowlands or ponds, thus lowering the water table in the vicinity as well as endangering the water supply for home or animal consumption. Lakes close to cities are even emptied as mere pails of water; not to mention the forest devastation on rocky terrain and on slopes of non-arable land, and the pollution of rivers upon any pretext whatsoever, etc. Some scientists are also worried about the ultimate effects on the biological balance of the universal use of toxic substances on soils, crops, forests. Similar fears could be entertained as regards the destruction, by millions of tons each year, of organic matter, an essential element of soil fertility and food production.

These examples of reckless squandering are sufficient to prove that the national conscience is not yet awakened to the necessity of conservation. Education of populations at all levels is consequently the first step in that direction. As Victor Van Straelen says: "Nous devons marcher vers des étapes toujours croissantes d'organisation et de conscience. *La continuité de la civilisation est à ce prix.*" This is true for every country, Canada included. In order to preserve our common heritage, we must decide on a national conservation policy, integrating all resources, with the active collaboration of all governments, be they federal, provincial, or municipal, and of other public bodies. This is the foundation not only of continuous prosperity for centuries to come, but above all of the survival of our nation.

In building up the future of Canada, biologists should be called upon to supply basic materials and guiding principles. Logically, when life is at stake, biologists must come first. I do not know of more competent advisers: they possess the knowledge to deal with all forms of life, have given ample proof of their ability to solve these difficult problems; besides, they have a

clear conscience of their duties toward the nation. Biologists must be the first architects of the future.

In conclusion, reverting to my opening remarks: I sometimes imagine that should Malthus be our contemporary, our Selection Committee would not fail to invite him to join our ranks, for truly, this economist was in fact a biologist who ignored himself. Thanks to the solemn warning he wrote on the wall of destiny, the future of humanity may yet be agreeable, nay even be brilliant, if we only read after him the signs in the stars and take action accordingly.

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SECTION FIVE

The Relation of Stress to Hemorrhage and Prothrombin Time Following Anticoagulants

L. B. JAQUES, F.R.S.C., G. J. MOGENSON, and L. M. FISHER*

A PUZZLING problem in the use of anticoagulants clinically has been the occurrence of hemorrhage. In the classical experiments of Murray, Jaques, Perrett, and Best (1937) on heparin and thrombosis in animals, it was remarked that hemorrhage was never observed even though the blood was incoagulable for considerable periods of time. We also observed this with dicumarol and other newer anticoagulants, for in many experiments on animals with prothrombopenic agents the prothrombin time was maintained at values of 2–10 minutes (normal 12–15 seconds) for months without any hemorrhage occurring. However, as soon as anticoagulants were introduced clinically, occasional hemorrhagic episodes were reported. In particular, while recommendations were followed regarding safe levels of the prothrombin time, many clinicians observed hemorrhage in a few patients on anticoagulants when the prothrombin times were only moderately elevated, yet other patients showed very elevated prothrombin times without hemorrhage. We did observe a severe hemorrhagic reaction in 1948 in two dogs of our colony when on anticoagulants. One of these occurred when the animal suffered an anaphylactic reaction with anti-distemper vaccine, the other occurred with a superficial infection. In 1953, Lepp, Chubaty, and Jaques reported that, in rabbits, frostbite together with anticoagulants produced a high incidence of hemorrhagic death. These observations suggested the possibility of identifying experimentally the apparently extraneous factors which precipitate hemorrhage in patients or animals maintained on anticoagulants. Frostbite or cold injury suggested the possibility of stress as a factor. Experiments have therefore been conducted on the combined effect of stress and anticoagulants in rabbits and rats.

Methods

Animals used were the ordinary laboratory stock animals.

Chemical stress agents used were 10 per cent NaCl intraperitoneally, 4 per cent formaldehyde subcutaneously, and insulin subcutaneously to produce convulsions, relieved immediately by injection of glucose. On the recommendation of Dr. H. Selye, doses used were just short of the M.L.D.

*Assisted by grants from the Defence Research Board of Canada. We are indebted to Mr. W. Chubaty for technical assistance.

in each case. These proved to be: for rabbits, 50 cc. of 10 per cent NaCl intraperitoneally, 55 cc. 4 per cent formalin subcutaneously, 720 units of insulin subcutaneously; and for rats, 4.5 cc. of 10 per cent saline intraperitoneally, 4.0 cc. of 4 per cent formaldehyde subcutaneously, and 280 units of insulin subcutaneously.

Frostbite was produced in rabbits by removing the fur with a depilating agent from one foot and immersing the foot in a mixture of dry ice and alcohol under general anesthesia. Rats were placed in cages in the cold room (—20°C) for approximately thirty minutes.

Psychological stress procedures used were electrification of the water source, exposure to high-pitched sound, and induction of seizure by electric stimulation. For the electrified water source, rats were placed in individual cages wired in such a way that they received shocks when attempting to drink. One electrode was attached to the cage and the other was introduced into the water through the rubber stopper of the water bottle. Sodium chloride was used as an electrolyte. The current was controlled by a transformer and set at 35 volts, 60 cycle. For two hours each morning the experimental animals as well as the control animals were allowed to drink and were fed. The lights in the room were on during this time. For exposure to sound, rats were subjected to a single exposure to high frequency sound. They were placed in an aluminum box 12″ × 10″ × 10″ with a lucite lid, having a Hartmann whistle introduced in one end and connected to the compressed air. The whistle was adjusted at 13,000 cycles and was sounded for two minutes. For electrically induced seizures, an adjustable alternating current stimulator was used. The rats were confined in a plastic box 12″ × 12″ × 5″, microhm jelly was applied to the ears, small alligator clips were attached, and the current (120 volts) was applied for 0.4–0.6 secs.

Anticoagulants used were heparin, phenylindanedione (PID), and dicumarol. Heparin (Connaught) was administered to rabbits 2,000 units (0.2 ml.) intravenously every eight hours for five days. Phenylindanedione was given orally 25 mg./Kg. three times a day following an initial dose of 100 mg./Kg., and dicumarol as a single dose of 5 mg./Kg. Rats received dicumarol daily in the food for the duration of the experiment at a dose level of 10 mg./Kg. body weight, care being taken to ensure complete ingestion of the prepared food.

Prothrombin times were determined by a modified Quick technique using undiluted plasma, M/40 calcium chloride, and commercial rabbit brain thromboplastin. Blood samples were taken from rabbits from the marginal ear vein and from rats by cardiac puncture after light ether anesthesia.

Hemorrhage in Rabbits

Approximately 230 rabbits have received anticoagulants and stress agents alone and combined. The results are shown in Table I. In rabbits

given these anticoagulants alone, death from hemorrhage occurred only with dicumarol. With the stress agents alone, the mortality was 6/30, 4/28, 0/21. However, when the animals were subjected to stress together with indirect anticoagulants (phenylindanedione or dicumarol), there resulted a high incidence of hemorrhagic death. Taking the totals, stress alone gave a mortality of 10/79, of which none were deaths due to hemorrhage but all were deaths in shock due to the immediate action of the stress agent. With anticoagulants alone, 10/75 rabbits died of hemorrhage. When the two agents were administered together, the mortality was 54/119 (45 per cent). Further, the time of death was quite consistent. It was the evening or night of the third day after receiving anticoagulant and stress agent. On autopsy, the consistent finding in the gross in the 58 rabbits was hemorrhage in the lungs, with little of note in other tissues. Microscopically, the lungs showed either marked oedema and vascular congestion or extensive early acute hemorrhagic bronchopneumonia. Such hemorrhagic death was not observed with heparin. It is, of course, difficult to compare the degree of blood incoagulability produced by heparin and the indirect anticoagulants. However, in the case of frostbite, it was previously reported that phenylindanedione delayed the onset of gangrene (3.1 days for control, 5.8 with anticoagulants). In the present series with heparin, the values were 2.9 for control, 4.1 for heparin, indicating the dose of heparin had the same effect as the indirect anticoagulant in this respect.

TABLE I

INCIDENCE OF HEMORRHAGIC DEATH IN RABBITS

Stress agent	Anticoagulant			
	None	Heparin	Phenylindanedione	Dicumarol
None		0/21	0/18	10/57
Insulin	6/30	0/10	19/26	3/12
NaCl	4/28	5/29	7/12	11/35
Frostbite	0/21	1/23	11/25	3/9

Stress alone	10/79	(non hem.)	= 13%
Indir. A.C. alone	10/75	(hem.)	= 13%
Indir. A.C. and stress	54/119	(hem.)	= 45%
Heparin and stress	6/62	(hem.)	= 10%

Hemorrhage in Rats

If the finding in rabbits is of general biological significance, it should be demonstrable in other species. We have therefore conducted studies in rats, and, as shown in Table IIA, it is possible to demontrate a mortality of approximately 50 per cent due to hemorrhage when stress together with anticoagulants is administered. With the stress agent alone, the mortality was 2/15; with dicumarol alone for 5 days, 0/14; with dicumarol for 5

days and stress on the second day, 9/21. However, we have found that a number of factors in the experiment influence the outcome, as shown in Table IIB. Eighty rats were taken in groups of ten. Instead of dicumarol being given as a single dose each day, it was given in the form of 5 g. of pellets containing 1:2,500 dicumarol which were eaten by the rats between 9 A.M. and 2.30 P.M. each day. These pellets were supplied for 15 days. Ten of the rats were females, all other groups males. Thirty rats were subjected to cardiac puncture on the fifth day for prothrombin times and forty to NaCl stress on the eighth day. The rats were followed for mortality up to 21 days. The results are summarized in the table. Mortality from hemorrhage on dicumarol daily for 15 days was 0/60 on the fifth day, 0/30 on eighth day, 0/10 on ninth day, 6/10 by thirteenth day. When rats on dicumarol were subjected to cardiac puncture on the fifth day, the immediate mortality was 6/30 but there was no further mortality in the survivors, all remaining alive on the thirteenth day. This represented a marked reduction in mortality of rats receiving dicumarol when compared with similar rats not exposed to cardiac puncture on the fifth day, suggesting that the latter had had some protective effect. When stress on the eighth day was imposed on dicumarol-treated rats, the immediate mortality was 16/19. Immediate mortality from stress alone was 0/20. It is evident that

TABLE II

MORTALITY FROM STRESS AND ANTICOAGULANTS IN RATS

A. 10% NaCl intraperitoneally	2/15
Dicumarol (10 mg/Kg.) daily for 5 days	0/14
Dicumarol daily + 10% NaCl on 2nd day	9/21

B. Dicumarol 15 days	Cardiac puncture 5th day	10% NaCl on 8th day	Deaths			
			to 6th day	to 8th day	to 9th day	11th–13th day
+	−	−	0/60	0/30	0/10	6/10 (60%)
+	+	−	6/30*	→	→	0/24 (0%)
+	−	+	→	0/19	16/19	— (85%)
−	−	+	→	→	0/20	3/20 (15%)

C. Dicumarol 5 days	Pretreatment	Controls	Electric shock on 3rd day
+	−	11/29 (38%)*	32/50 (64%)*
+	Previous cardiac puncture	11/47 (30%)*	12/37 (32%)*

D.	Dicumarol	Adrenalectomized	Adrenalectomized +Dicumarol
	6/100	0/6	18/18

*Deaths due to cardiac puncture and resulting tamponade. Other deaths due to spontaneous hemorrhage, chiefly into the lungs.

three parameters for hemorrhagic death in rats are available for study—the spontaneous hemorrhage and mortality on the thirteenth day from anticoagulant alone, the hemorrhage and mortality following stress on the eighth day, and death following the severe trauma of cardiac puncture. The previous history of the animals (cardiac puncture for blood samples, etc.) may affect the incidence of mortality from these procedures. In Table IIC are shown similar results with electric shock. The mortality from cardiac puncture was 11/29 (38 per cent) for rats receiving dicumarol (about the same as that from cardiac puncture alone shown in Table IIB), but was 32/50 (64 per cent) with dicumarol and electric shock. Evidently the electric shock markedly increased the mortality from cardiac puncture. However, in the case of rats previously subjected to cardiac puncture for blood studies, there was no difference in the percentage of mortality (30 and 32 per cent). As reported in Table IID, adrenalectomized rats showed a marked susceptibility to anticoagulants, all dying of hemorrhage within a week. It is evident that, by subjecting the animals to a stress agent and an indirect anticoagulant simultaneously, a high incidence of hemorrhagic death could be produced in rats as in rabbits. Also as in rabbits, the most obvious gross pathological lesion in the rats was blood in the lungs—hence the term "hemorrhagic death."

Coagulation Changes in Stress

Concomitant with these studies have been determinations of the clotting system of the same animals. In rabbits, stress procedures alone had no effect on the values for the one-stage, the modified two-stage or the unmodified two-stage procedures for prothrombin time. As regards changes in prothrombin time with dicumarol, rabbits can be divided into susceptible and non-susceptible groups (Link, 1943–1944). Forty-four rabbits were tested with 5 mg. dicumarol/Kg. and classified on the basis of no change in prothrombin time (non-susceptible), increased prothrombin time but less than 25 seconds (moderately susceptible), increase in prothrombin time to over 25 seconds (highly susceptible). As shown in Table III, on giving dicumarol alone in this test, the mortality was slight in the first two groups but high in the last group. When dicumarol was repeated together with

TABLE III

MORTALITY OF RABBITS ON ANTICOAGULANT AND STRESS

Prothrombin time response to dicumarol	(1) Dicumarol	(2) Dicumarol+10% NaCl (survivors of (1))	Over-all mortality
no change	0/5	2/5	40%
<25″	1/15	7/14	50%
>25″	9/24	6/15	63%
	10/44	15/34	25/44

TABLE IV

EFFECT OF STRESS AGENTS ON PROTHROMBIN TIME IN RATS

Treatment	Controls (mean±s.d.)	Treated (range)	t value	p
Cold (−20°C)	15.9±0.6	23.1−30.6	7.1	<0.01
Insulin convulsions	17.3±2.0	21.0−48.0	6.9	0.05−0.01
10% NaCl intraperit.	18.6±1.9	24.6−36.0	5.2	0.05−0.01
4% formaldehyde subcut.	18.6±1.8	19.4−36.0	3.6	0.05−0.01
Electric shock	14.2±0.6	13.1−22.8	3.2	<0.01
Discrimination breakdown	16.6±0.6	13.4−33.0	100*	<0.01
Audiogenic seizures	17.2±2.6	20.3−28.8	6.9	<0.01
Frustration (electrified water source)	17.7±1.2	14.8−25.2	8.5*	<0.01
Electric shock with dicumarol	22.8±8.7	14.0−135.0	4.2	<0.01
Electric shock with dicumarol and previous cardiac puncture	23.5±9.3	14.0−57.2	1.0	<0.10

*Fisher's *F* value

the stress agent, there was a marked increase in mortality in the moderately susceptible group. Analyses were performed for one-stage, modified two-stage, and unmodified two-stage tests, for prothrombin time and for dicumarol plasma levels. No consistent significant difference was observed for these levels compared with and without stress for the individual rabbits in any of the groups.

In rats (as shown in Table IV) stress alone increased the prothrombin time in many animals. This was observed with cold, insulin convulsions, NaCl intraperitoneally, formaldehyde subcutaneously, and electric shock. In our initial experiments, the increase in prothrombin time with stress was surprisingly consistent. However, with further experience, we found that this does not always occur. Rather, as shown with the values for electric shock, some rats (in this case 50 per cent) gave a marked increase (much more than twice the standard deviation for the mean of the control values) but other rats showed no change in the prothrombin time. However, using the "t" test or Fisher's *F* value, it can be shown that the increase, when it does occur, is highly significant. The increase in prothrombin time also occurred with such psychological procedures as frustration (with an electrified water source), discrimination breakdown (in forced jumping), and audiogenic seizures. Coagulation tests carried out on these rats demonstrated that the increase in one-stage prothrombin time was due to a decrease in proconvertin. As shown in Table IV, the previous history of the animal can interfere with the increase in prothrombin time following the application of stress. In the lowest portion of Table IV, rats on dicumarol were subjected to electric shock. The latter resulted in a further

increase in prothrombin time, indicating that dicumarol did not interfere with the effect. However, previously subjecting the rats to cardiac puncture resulted in no increase in prothrombin time occurring with stress.

Discussion

A high incidence of hemorrhagic death (50 per cent) was observed when anticoagulants (phenylindanedione, dicumarol) were administered to rabbits and rats subjected to stress (insulin shock, 10 per cent NaCl intraperitoneally, frostbite), compared to the negligible mortality from hemorrhage with these agents separately in the doses used. On post mortem, the main pathological changes were found in the lungs. In the case of frostbite, hemorrhage was also frequently observed in the frostbitten areas. Less frequently, hemorrhage was observed from the mouth, gastrointestinal tract, and other areas. In rabbits for which we obtained hematocrit values, there was a steady fall in the hematocrit, a finding we have encountered frequently in animals with a persistent increased prothrombin time due to vitamin K deficiency, prothrombopenic agents, etc. In the latter case, H. P. Wright and Hayden (1955) have shown from microscopic tissue studies that this is due to a leakage of red cells from the circulation. There was a significant correlation between falling hematocrit values and mortality. No changes in coagulation were observed with stress in rabbits as judged by changes in prothrombin time and the stress agent did not significantly affect the action of dicumarol on prothrombin time and coagulation factors in rabbits. Stress agents caused an increase in prothrombin time in rats because of a decrease in proconvertin, and previous cardiac puncture abolished the extra increase both in prothrombin time and in mortality due to a stress agent.

Hemorrhage represents a defect in hemostasis. Hemostasis—the prevention of loss of blood when a break occurs in the circulation—is provided by three separate, mutually supporting mechanisms in mammals. These are fibrin formation or the coagulation system of the blood plasma, platelet agglutination or the plugging action of the blood cells, and vascular constriction or the active response and integrity of the blood vessel itself. In general (and this has been established many times both experimentally and clinically), defect in one of these mechanisms is not accompanied by serious hemorrhage, but if more than one mechanism is interfered with, hemorrhage is serious and most difficult to stop. Recently Kramár, Meyers, and Wilhelmj (1955) have made measurements of capillary resistance after stress in various species. Rats and rabbits differed in their immediate response, but, for both, the most common late result was a marked decrease in capillary resistance, which, starting the third day, persisted for several weeks after stress. This would fit in time with the period when hemorrhage and death occurred in our animals. Further, the incidence of cases (about 50 per cent) showing the decrease in capillary resistance agrees with the incidence of mortality we observe. Adrenalectomy abolished capillary

resistance in the rats of Kramár, Meyers, and Wilhelmj and caused a 100 per cent mortality on anticoagulants in our hands. We therefore suggest that, once again, we see in these experiments the serious effects of interference simultaneously with two mechanisms of hemostasis: interference with capillary resistance by stress agents at the same time as interference with coagulation by anticoagulants.

Conclusions

1. A high incidence of hemorrhagic death was observed in rabbits and rats subjected to stress agents together with indirect anticoagulants (dicumarol or phenylindanedione). This was not observed with heparin tested in rabbits. Previous cardiac puncture in rats abolished the increase in mortality due to stress. Adrenalectomy in rats resulted in 100 per cent mortality with dicumarol alone.

2. No changes in the coagulation system could be detected in rabbits with stress. In rats, stress agents caused an increase in prothrombin time and this appeared to be significantly related to mortality.

3. It is suggested that the mortality observed in rats and rabbits subjected to stress agents together with indirect anticoagulants is due to the combined effect of the stress agent decreasing vascular resistance and the indirect anticoagulant interfering with coagulation. The two together represent an overwhelming damage to hemostatic mechanisms.

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TRANSACTIONS OF THE ROYAL SOCIETY OF CANADA

VOLUME L : SERIES III : JUNE, 1956

SECTION FIVE

Floral Transgression of Major Geological Time Zones

NORMAN W. RADFORTH and GLENN E. ROUSE

Presented by H. B. SIFTON, F.R.S.C.

Introduction

EARLY investigations of fossil plant assemblages from the geological record have resulted in the recognition of floral conspecti which appear to be representative of certain time intervals. Identification of these characteristic floras has arisen through rather thorough examinations of collections of fossil plants from the time intervals, and has provided the basis for our knowledge concerning the distribution of fossil plants throughout the geological column.

In recent years, plant microfossils (chiefly spores and pollens) have assumed an increased significance in palaeobotanical and geological studies. Features of plant microfossils which relate to their importance include the following: (1) Microfossils are generally diagnostic of the plants or plant groups with which they were originally associated. (2) The structure and chemical composition of plant microfossils has allowed for preservation in most sediments, including some in which macrofossils are not sufficiently recorded to be useful. (3) Of the microfossils, most pollens and many spores are produced in relatively large numbers, and are well adapted for dispersal over wide areas by either wind, water, or insects. The recognition of these three principles has provided the essential stimulus and direction to microfossil investigations, from which much valuable information has been gained.

Early investigations established the utility of plant microfossils in phylogenetic and stratigraphic problems. Recent studies have revealed that microfossil assemblages contained within selected coals and mineral strata can be utilized for the assessment of palaeoecology and sedimentation processes (Hunger, 1953; Traverse, 1955; Rouse, 1956). It is expected that as additional information on the occurrence, association, and distribution of microfossils is obtained, the microfossil record will supplement that of the macrofossil in providing evidence of floral migration and data for palaeoecology. Thus microfossils have a potential application to the understanding of geographic and stratigraphic migrations of floras, comparable to the application of macrofossils in assessing floral distributions within, for example, the Tertiary (Axelrod, 1952; Chaney, 1938; Dorf, 1955).

The principle of establishing floral ranges on the basis of plant micro-

fossil distributions has been limited to several investigations. In each case, the ranges have encompassed only short intervals of geologic time, and, to the authors' knowledge, no attempt has previously been undertaken to assess long-range distributions of plant groups on the basis of known occurrences of microfossils. The primary objective of this paper is to indicate how recent microfossil evidence enhances our knowledge of floral overlap and floral transgression of major geological time boundaries. The development of this objective is assisted by the presentation of an illustration of short-range overlap of Cretaceous and Tertiary microfossils, together with a compilation of known distributions of selected microfossils throughout the geological column.

Representative Floras

Palaeobotanical analyses which have been conducted on all continents for over a century have indicated that certain plants and plant assemblages characterize the flora of particular geological time intervals. Examples of representative floras include the Upper Devonian–Mississippian, the Pennsylvanian, the Permo–Triassic, and the Juro–Cretaceous. As might be expected, degrees of overlap exist between representative floras, so that some groups are often found well outside the time range of the representative floras. In addition, differences are found in the kind and frequency of plants from different locations within the same floral-time zone. Nevertheless, the over-all distribution of fossil plants has shown that certain associations are characteristic of particular intervals, and has resulted in the recognition of representative floras.

Investigations of microfossil assemblages from rocks of most ages have revealed that conspecti of microfossils are found within certain time intervals which appear to be representative of particular zones. However, recent studies on early Palaeozoic and later Mesozoic material have indicated that some microfossil forms representing natural plant groups have much greater ranges than have been previously recognized on the basis of macrofossil evidence (Rouse, 1956).

Because of our lack of knowledge on microfossil-macrofossil relationships, it is difficult to assess the degree of affiliation, if any, which exists between the macroflora and the microflora from the *same* geological time interval. However, there is evidence that, in most fossiliferous deposits, there occur more identifiable microfossil forms than macrofossil, and it is possible that the microflora will of necessity be the representative floral character for intervals having few identifiable macrofossils.

It is also possible that, in some cases, representative microfloras and representative macrofloras do not relate to the same boundaries within the same time ranges. This is suggested in examinations of micro- and macrofloras of several time intervals: for example, the Mississippian and Juro-Cretaceous, where the boundaries of representative microfossil conspecti do not appear to coincide with those macrofloras previously designated as representative.

Stratigraphic Ranges of Microfossils

The results of several investigations have established stratigraphic ranges of plant microfossils within coal measures and sedimentary strata. Noteworthy are the ranges presented for the Devonian of the Russian platform (Naumova, 1953; Novik 1954); the Mesozoic of Europe (Thiergart, 1949); and the Tertiary of Europe (Thiergart, 1940; Potonié, 1951). These investigators have indicated the range of various plant microfossils, and have shown that certain forms have restricted ranges, whereas others extend throughout the time intervals examined. The fact that particular microfossils are restricted in range allows for the delimitation, correlation, and dating of strata.

Recent examinations of selected Cretaceous and Tertiary material from Canada have enabled the authors to present the occurrence and range of particular microfossils, and to illustrate by example that certain microfossils representing natural plant groups transgress one intra-periodic time boundary as well as one inter-periodic boundary. As an illustration of this transgression, the occurrence and distribution of thirty-three plant microfossils have been plotted for the six strata investigated, and are shown in Chart I. Photographs of the microfossils corresponding to the figure numbers given in Charts I and II are arranged in the photographic plate, and are numbered from 1 to 42. In most cases, the names of the microfossils indicate a natural affiliation where that is known. Some forms were recently named and described by the junior author (Rouse, 1956); others are specimens which are identical with previously described microfossils. The alphabetical-numerical designations are those assigned to the microfossils in accordance with the system outlined by Radforth and Rouse (1954).

An examination of Chart I reveals that two spores (*Sphagnum antiquasporites*—S_4 and *Osmunda-sporites primarius*—T_1 T_8) occur in all six strata, and range from the Lower Cretaceous to the Tertiary. Most of the other microfossils occur in strata of two ages; that is, they are found in the Lower and Upper Cretaceous, or in the Upper Cretaceous and Tertiary. Several forms are common to only the Lower Cretaceous and Tertiary. There are other microfossils which are limited in occurrence to strata of one age; for example, the following are limited to the Upper Cretaceous: *Aquilapollenites quadrilobus*—N_2; *Laevigato-sporites ovatus*—O_4; P_{10}—unknown affiliation; *Sparganium globipites*—Q_9; *Tricolpopollenites divergens*—Q_{15}; *Sporites neddeni*—S_{45}; *Pollenites laesus*—U_2; *Elytranthe striatus*—U_5; U_{11}—unknown affiliation; *Polypodiaceae-sporites favus*—V_3.

A further analysis of Chart I discloses several significant features. (1) Many of the microfossils indicate floral overlap because of their range from the Lower to the Upper Cretaceous. (2) The fact that particular microfossils are confined to the Upper Cretaceous, whereas others are limited to the Lower Cretaceous, indicates that Upper and Lower Cre-

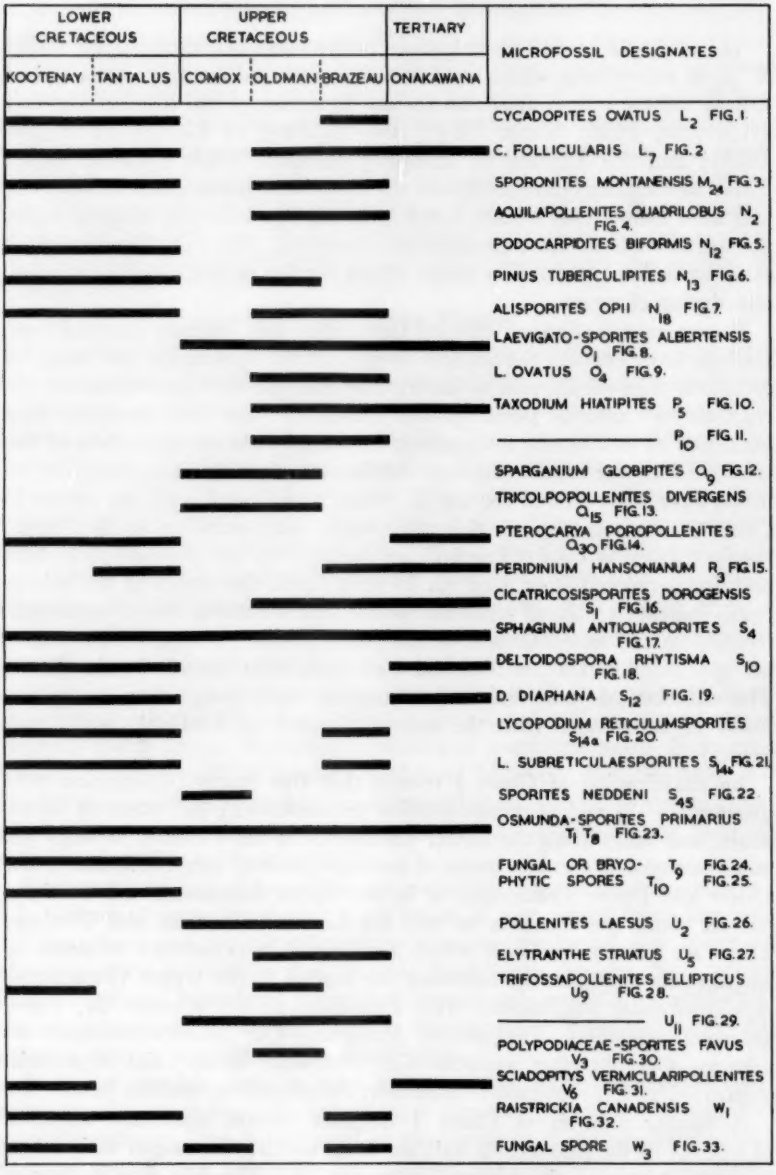
LOWER CRETACEOUS
UPPER CRETACEOUS
TERTIARY
KOOTENAY
TANTALUS
COMOX
OLDMAN
BRAZEAU
ONAKAWANA
MICROFOSSIL DESIGNATES
CYCADOPITES OVATUS L2 FIG. 1
C. FOLLICULARIS L7 FIG. 2
SPORONITES MONTANENSIS M24 FIG. 3.
AQUILAPOLLENITES QUADRILOBUS N2 FIG. 4.
PODOCARPIDITES BIFORMIS N12 FIG. 5.
PINUS TUBERCULIPITES N13 FIG. 6.
ALISPORITES OPII N18 FIG. 7.
LAEVIGATO-SPORITES ALBERTENSIS O1 FIG. 8.
L. OVATUS O4 FIG. 9.
TAXODIUM HIATIPITES P5 FIG. 10.
P10 FIG. 11.
SPARGANIUM GLOBIPITES Q9 FIG. 12.
TRICOLPOPOLLENITES DIVERGENS Q15 FIG. 13.
PTEROCARYA POROPOLLENITES Q30 FIG. 14.
PERIDINIUM HANSONIANUM R3 FIG. 15.
CICATRICOSISPORITES DOROGENSIS S1 FIG. 16.
SPHAGNUM ANTIQUASPORITES S4 FIG. 17.
DELTOIDOSPORA RHYTISMA S10 FIG. 18.
D. DIAPHANA S12 FIG. 19.
LYCOPODIUM RETICULUMSPORITES S14a FIG. 20.
L. SUBRETICULAESPORITES S14b FIG. 21
SPORITES NEDDENI S45 FIG. 22
OSMUNDA-SPORITES PRIMARIUS T1 T8 FIG. 23.
FUNGAL OR BRYO- PHYTIC SPORES T9 T10 FIG. 24. FIG. 25.
POLLENITES LAESUS U2 FIG. 26.
ELYTRANTHE STRIATUS U5 FIG. 27.
TRIFOSSAPOLLENITES ELLIPTICUS U9 FIG. 28.
U11 FIG. 29.
POLYPODIACEAE-SPORITES FAVUS V3 FIG. 30.
SCIADOPITYS VERMICULARIPOLLENITES V6 FIG. 31.
RAISTRICKIA CANADENSIS W1 FIG. 32.
FUNGAL SPORE W3 FIG. 33.

CHART I. Stratigraphic distribution of selected plant microfossils in Cretaceous and Tertiary strata of Canada.

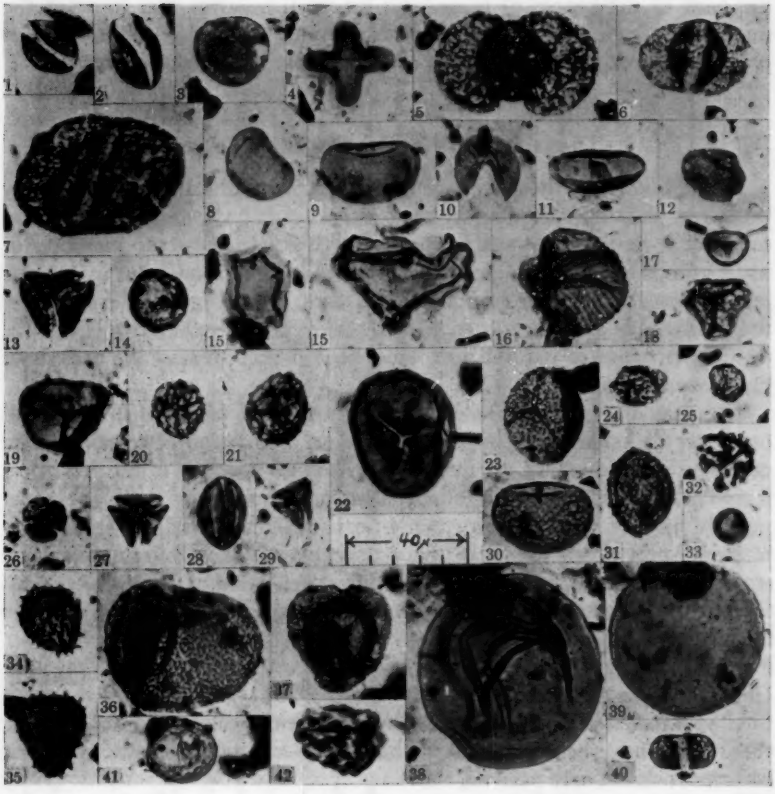

PLATE I

taceous horizons can be delimited on the basis of the occurrence of these diagnostic microfossils. (3) The absence from the Comox of many of the microfossils which are present in the other two Upper Cretaceous strata indicates that the flora which existed in the region of the deposition of the Comox coals (Vancouver Island) was distinct from that of the western interior. The fact that the Comox is approximately correlative to the Oldman and Brazeau formations, coupled with the distinctiveness of the microfossil assemblages, suggests either extensive floral migration, radically different ecological conditions, or possibly a combination of both during the interval of deposition represented. (4) The number of microfossils common to the Kootenay and Tantalus indicates that these two formations

contain similar floras, supports the contention that the two horizons are correlative, and suggests a uniformity of the flora over a wide geographic region. (5) The separation of the Upper and Lower Cretaceous strata on the basis of differences in microfossil conspecti suggests that some of the microfossils have a potential application as index microfossils. This is particularly evident in the case of several Upper Cretaceous forms.

Transgression of Major Time Zones

In addition to their importance in stratigraphical and migratory problems, plant microfossils may be of assistance in indicating the geological range of various plant groups, in showing that at least some members of plant groups have transgressed major geological time zones, and in suggesting greater antiquity for several natural taxa. As preliminary evidence of the potentiality of this concept, actual occurrences of selected microfossils, as representatives of natural taxa, have been plotted against the periods of the geological column.

The principle of floral transgression is influenced by three fundamental concepts: (1) that evolution, extinction, and progression of certain plants, or groups of plants, have occurred throughout the life span of the geological record; (2) that floral migrations have taken place in most geological periods, thereby accounting for many floral differences and the recognition of floral provinces; (3) that the conspectus of plant microfossils in a stratum representing a given time is a direct reflection of the flora, and indirectly an indication of the ecology and sedimentation associated with the development of that flora.

The known geological distribution of selected microfossils is shown in Chart II. The eighteen microfossils were chosen because of their recent disclosure in Cretaceous and Tertiary strata from Canada, and also because these forms have been reported in the past as occurring in either older or younger rocks. Where possible, the macrofossil or modern taxonomic group with which the microfossils are most closely affiliated is stated. In addition, figure numbers of representative microfossils are given to facilitate recognition of the morphological characters.

Pteridophyte Spores

An examination of Chart II indicates that the genera *Laevigato-sporites* and *Raistrickia* have an unbroken range from the Pennsylvanian to the Recent. Three other pteridophytic spore genera, *Acanthotriletes*, *Microreticulati-sporites*, and *Perotrilites* (which includes the Pennsylvanian forms of *Denso-sporites* and *Anulati-sporites*) range from the Pennsylvanian to the Upper Cretaceous, although their occurrences are unreported in at least part of the range. With the exception of a break in the Permian, spores of *Osmunda-sporites* occur in all ages from Devonian to Recent.

CHART II. Ranges of various plant groups based on known occurrences of plant microfossils.

Gymnosperm Pollens

Pollen grains assigned to the bennettitalean-cycadalean complex have been recorded in strata from Permian to Tertiary. Bladdered pollens of coniferous affiliation have a beginning in late Pennsylvanian-Permian strata, and assume apparent relationships to modern coniferous taxa in the Jurassic.

Angiosperm Pollens

Pollens assigned to *Betula* and *Pterocarya* occur in the Cretaceous, whereas the occurrence of *Juglans* pollens is limited to the Tertiary. The occurrence of a tricolpate pollen in a Jurassic sediment reported by Erdtman (1948) probably represents the earliest record of the angiosperms, although recent discoveries by Naumova (1950) of tetra-porate grains resembling modern *Alnus* pollens from Mississippian strata of Russia suggest the possibility of a much older origin for the Angiospermae. The reference by Radforth and McGregor (1954) to pollen with angiospermous affinity in Devonian rocks is not regarded as conclusive by those authors.

Uncertainly Affiliated Microfossils

The recent disclosure of "Sporangites" and *Tasmanites* from Cretaceous and Tertiary strata has projected the range of these forms which have previously been limited in occurrence to Devonian and early Mississippian horizons. The fact that both of these microfossils are generally found in semi-marine or lacustrine deposits suggests the hypothesis that they actually ranged from the Devonian to the Cretaceous, but were previously unrecorded because of their association with the particular sedimentary environments.

The pollen form assigned to *Pityopollenites* is identical with the pollen from *Caytonanthus*, a Rhaetic-Jurassic genus of male fructifications affiliated with the Caytoniales. The appearance of this pollen in Cretaceous and Tertiary horizons extends the previously known range.

The affiliation of the microfossils with the natural taxa in Chart II deserves qualification. It might be construed that the natural taxa linked with the microfossils indicate natural relationships. In some cases (for example, *Sphagnum*, the Coniferales, and the Angiospermae) this is true. However, in other instances (for example, *Acanthotriletes-Pteridium*, *Microreticulati-sporites*-Noeggerathiales, and *Perotrilites*-Selaginellaceae) the affiliations are qualified. This is necessary, because these latter microfossil genera possibly represent several natural plant groups, and the actual relationships are in doubt. However, the microfossil forms from the younger periods are generically and sometimes specifically identical with microfossils from older periods. This is the case with all of the microfossil genera listed. Because microfossils are generally diagnostic of natural plant relationships, it is probable that many of the plant groups actually extended within the

ranges indicated. Thus it is probable that several groups, for example the Polypodiaceae and the Osmundaceae, had representatives at an earlier time in geological history than has previously been realized. The recognition of this probability of greater antiquity should provide a fruitful field for future research in palaeobotany.

It should be realized in the examination of the ranges presented here that there are many other microfossils from the geological record which are limited to specific periods, and do not apparently transgress geological time zones. However, as information concerning microfossil occurrence and distribution increases, the recognition of transgression of time boundaries is becoming more apparent. This phenomenon is suggesting that biological tolerance has played an important role in the survival and extinction of plants throughout major environmental change in the geological record.

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SECTION FIVE

Antiquity of Form in Canadian Plant Microfossils

NORMAN W. RADFORTH and COLIN McGREGOR

Presented by H. B. SIFTON, F.R.S.C.

WITHIN the last decade there has been a tendency in palaeobotanical research to place a greater emphasis on the study of fossil spores and pollens, with relatively less emphasis on macrofossils. This shift has occurred because of the realization that plant microfossils provide a fertile area of enquiry for both the botanist and the geologist. They are obtainable in abundance from several types of rocks, representing sedimentary environments which extend in age from early Palaeozoic to Recent. Further, they tend to transgress boundaries of geological climate and sedimentary facies, and they possess distinctive structural features. In particular, the microfossils of the Palaeozoic era are significant, because they represent the periods of geological time when land plants presumably underwent their earliest evolutionary development.

Spores and pollens have been considered in various ways in the past. Many of the early works consisted of descriptions of their morphology and geological locus (4, 7). This approach is being re-emphasized at present by several oil and coal interests (6, 9). For Palaeozoic material, some speculation is frequently made as to biological affinity (14, 8), but with more limited success than can be obtained for microfossils from younger sediments.

The various schemes and opinions that have been advanced for the classification and nomenclature of plant microfossils have not been consistent in their selection and interpretation of diagnostic microfossil features. An appraisal of the variations and antiquities of features of spore and pollen form may contribute toward a greater unity of thought on this problem.

Recently, because of the discovery of greater quantities of spores and pollens, our knowledge of the scope of variation in the structure of Palaeozoic microfossils is becoming more complete. In Canada, a recent survey by the authors of a large number of plant microfossils occurring in Palaeozoic rocks has revealed the early presence of numerous structural entities that persist through time.[1] It is now appropriate, therefore, to re-

[1]In a previous paper (17), the authors discussed an assemblage of microfossils from sediments which had been logged as Upper Devonian. In it were several unusual microfossils, including a single example of a type resembling tricolpate angiosperm pollen (17, fig. 22). Additional checks have strengthened the view that this assemblage contains a

examine the ranges of form of Palaeozoic microfossils, and to assess them in relation to the geological time scale.

When we examine microfossils of various ages, without considering the questions of classification mechanics or biological relationships, we are able to chart the trends in features of form through time (Plates I and II). It is important to note that in doing this, we are setting aside phylogenetic considerations for the present, and are thinking of the occurrence, absence, and abundance of structural elements, or levels of structural complexity.

In addition to information derived from Canadian microfossils, the authors have drawn from the literature, particularly for data concerning the Cambrian, Ordovician, and Permian periods.

Occurrence of Features of Form in the Palaeozoic

Several simple features predominate in the most ancient sediments (Plate I). Small, thin-walled, circular and trilete forms are present very early in time, and tend to dominate in the assemblages of the Cambrian, Ordovician, and Silurian (1, 2, 3, 12, 13, 17, 18). Long, thin appendages are prominent in early deposits as well, particularly in Ordovician, Silurian, and Devonian marine sediments.

In the Upper Silurian and Lower Devonian, a number of more complex features arise nearly simultaneously. Reticulate and spinose exines first make their appearance here, along with large size, thick wall, and subtriangular shape. By Middle Devonian time, flanges, equatorial thickenings, contact areas, radial striations, and perispores become established.

Bladders, although they have been reported by one author as occurring in the Lower Silurian (13), are not truly established until the Upper Devonian (6, 14). Ornamentation in the form of ridges first appears in the Lower Devonian (Plate III, fig. 19), and is present in the Upper Devonian (17), the Lower Carboniferous (15), and the Upper Carboniferous (16). Pores, furrows, and bilateral symmetry arise in the upper part of the Palaeozoic.

For most features, there is a span of time in which the character is present in a relatively large number of individuals, that is, an interval in which there is a tendency toward predominance of the feature. Thus, the first five features presented in Plate I are characteristic for Cambrian, Ordovician, and Silurian microfossils, although they extend with greatly diminished importance completely through the Palaeozoic. Pronounced trends of abundance of features are no less evident for Devonian, Mississippian, Pennsylvanian, and Permian time. In most instances, there is an initial lag between first appearance and attainment of prominence of the feature. After the period of abundance, the feature declines in prominence and becomes a minor constituent of younger assemblages.

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mixture of Cretaceous and Pennsylvanian elements. Since a definite conclusion has not been reached as to the age of these microfossils, the authors have refrained from including them in the present discussion.

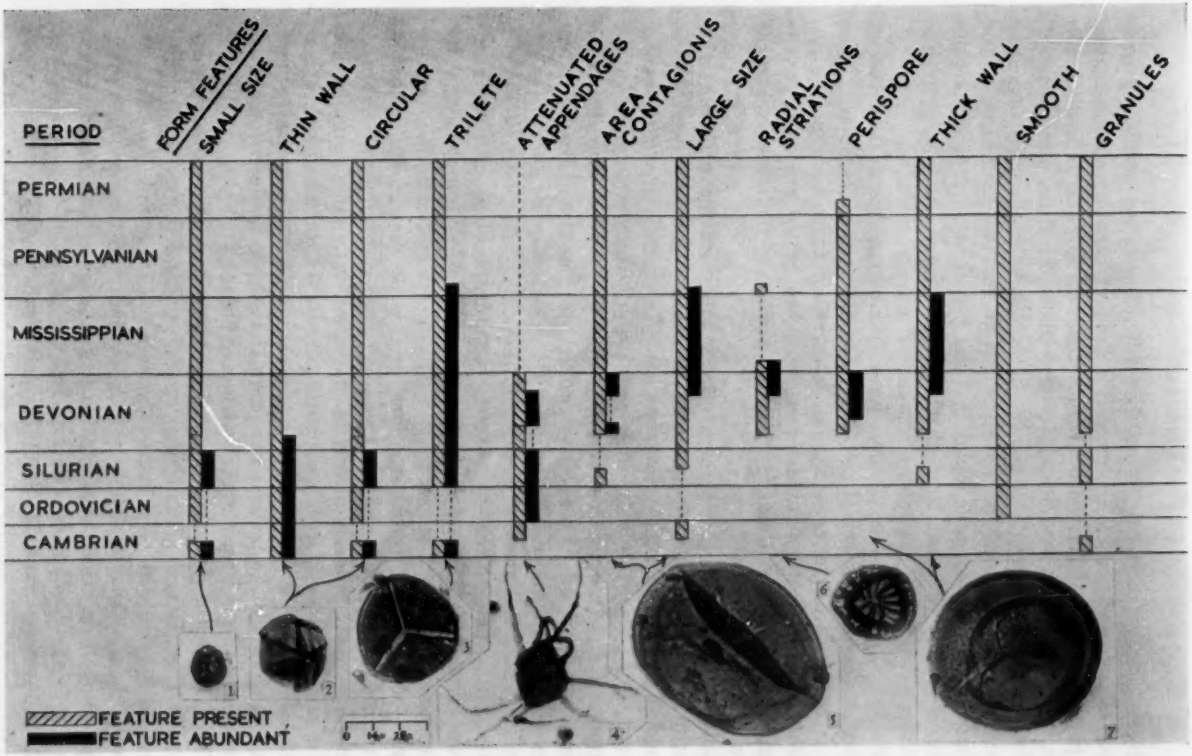

PLATE I. Range of form features in Palaeozoic plant microfossils.

Discussion

Hoffmeister *et al.* (6) point out that only a few of the possible environments of sedimentation are represented in the literature on microfossils, and in particular that of the Carboniferous coal-swamp. This is undoubtedly true, and subsequent modification of any charts based on present data is to be expected. However, the present authors have examined spores from several shale and sandstone environments within the Mississippian and Pennsylvanian periods, and found that the preponderance of the various features is little different from that experienced for coals of equivalent periods. Nevertheless, the species represented usually differ.

Working from the data of spore-form distribution, the authors suggest a method for dating assemblages of microfossils from rocks for which the age is not known. The conspectus of features within any assemblage can be checked against the dominant features shown by the graphs of feature distribution (cf. Plates I and II), and the position of the conspectus in the time scale can be assessed.

Subsequent to their initial establishment, most of the early-occurring structural entities noted here persist throughout all younger periods. In this respect they apparently differ from species, which usually arise and become extinct within relatively short intervals of time. The development of the perispore may be used as an example. This structure in some Devonian examples (Plate I, fig. 7) is of an order different from that in Pennsylvanian types (cf. the genus *Endosporites*).

It is possible that the distributions of abundance of features of form of spores and pollen correspond directly with distributions of prominence within certain life-forms, habitat-groups, or levels of complexity of the plants which produced the spores and pollens. For example, the high frequency of perispores, radial striations, and *areas contagionis* evident in the microfossils of the Devonian period will no doubt ultimately be traced to specific natural groups of plants, when evidence is found of organic union of the microfossils with their sporophyte parents. In the meantime, it may be distribution of spore form, even more than that of artificial genera, which can provide the better circumstantial evidence for interpretation of the ecology and phylogeny of the Palaeozoic flora.

The evidence of diverse microfossil features in early Palaeozoic sediments in Canada and abroad supports the contention that a diversified terrestrial flora existed even in the Cambrian. The several spore features shown to have existed in Cambrian, Ordovician, and Silurian time prove the presence, at that time, of plants that had adapted at least a part of their life-cycle in ways which are characteristic for plants of known terrestrial habit. It now seems probable that other plant features had become adapted in a corresponding manner even at this early period in time. Indeed, a similar suggestion has been postulated by Leclerq (11) and Høeg (5), mainly on the basis of the status of differentiation of the Silurian-Devonian macroflora.

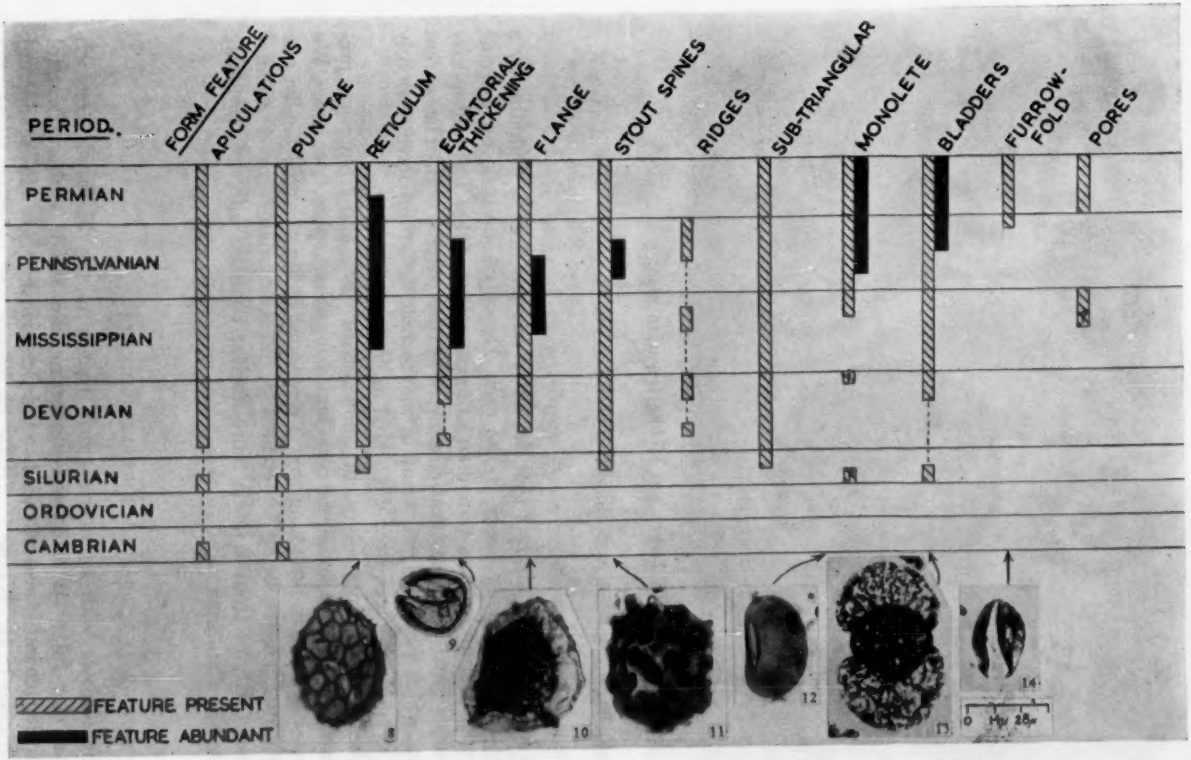

PLATE II. Range of form features in Palaeozoic plant microfossils.

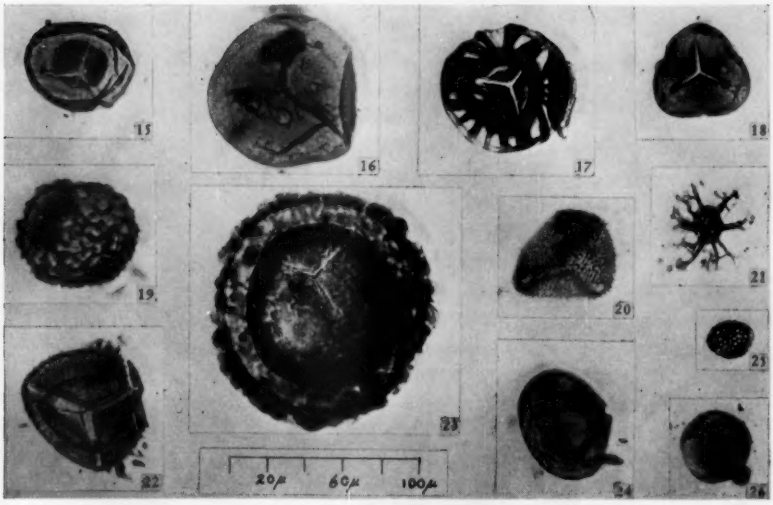

PLATE III. Lower and Middle Devonian plant microfossils.

Notwithstanding the fact that the latter vascular flora is undoubtedly a diverse one, the microfossils of the early Devonian illustrate an extreme diversity of form in some Canadian sediments (Plate III). The multiplicity of forms greatly exceeds that displayed by the macrofossils. The parent plants which produced this array of microscopic structures have obviously not, in most instances, been discovered as yet.

The question is not solved, of course, as to when and from what predecessors this diverse and apparently highly organized spore flora arose. We are now justified in proposing that it developed either polyphyletically, one of the lines possibly being represented by the Cambrian lycopod *Aldanophyton* (10), or from a much more ancient common ancestor, probably before the Cambrian.

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